
VEGETATION OF LIMESTONE AND DOLOMITE GLADES IN THE OZARKS AND MIDWEST REGIONS OF THE UNITED STATES¹

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ABSTRACT

Literature on the vegetation of limestone and dolomite (cedar) glades in the Ozarks of Missouri and Arkansas and in the midwestern United States (Illinois, Indiana, Ohio, Wisconsin) is reviewed. Dominant plants in these glades are C₄ perennial prairie grasses, of which little bluestem (*Schizachyrium scoparium* (Michx.) Nash) is the most important. Without removal of invading woody plants by fire or other means, succession in these rocky, calcareous openings is to forest. They differ from cedar glades in the southeastern United States, which are dominated by C₄ annual grasses (primarily *Sporobolus vaginiflorus* (Torr. ex Gray) Wood) and do not require management or natural disturbances to maintain them. We suggest that the anthropogenic, prairie-grass-dominated openings in the Ozarks and Midwest be called xeric limestone (or dolomite) prairies and that the term cedar glades be used for an edaphic climax dominated by C₄ summer annual grasses in natural openings on limestone or dolomite bedrock.

Key words: annual *Sporobolus* species, Midwestern (U.S.A.) limestone glades, Ozark glades, *Schizachyrium scoparium*, woody plant invasion, xeric limestone prairies

Although the climatic climax vegetation in the eastern United States is forest (Shreve, 1917; Braun, 1950; Küchler, 1964), long-persisting plant communities dominated by herbaceous angiosperms and/or cryptogams occur in areas where bedrock is exposed and/or soil depth in most places is too shallow to support trees or shrubs. Examples of these edaphic climax rock outcrop communities include the mid-Appalachian shale barrens (Platt, 1951; Keener, 1983; Braunschweig et al., 1999), granite outcrops of the southeastern piedmont (Oosting & Anderson, 1939; McVaugh, 1943; Keever et al., 1951; Burbank & Platt, 1964; Palmer, 1970; Shure, 1999), and the cedar (limestone) glades of the Central (Nashville) Basin in Tennessee (Quarterman, 1950; Baskin & Baskin, 1985; Somers et al., 1986; Drew, 1991) and of the southeastern United States in general (Baskin & Baskin, 1999).

The terms “cedar glades” and “limestone (or dolomite) glades” are also used to describe grass/forb-dominated openings over shallow limestone or dolomite soil on ridgetops and side slopes in the Ozarks (Steyermark, 1940; Erickson et al., 1942; Kucera & Martin, 1957; Ladd & Nelson, 1982; Nelson & Ladd, 1983; Nelson, 1985; Fig. 1) and Midwest (e.g., Curtis, 1959; Kurz, 1981; Aldrich et al., 1982; Heikens & Robertson, 1995). Thus, the

use of these terms in the Ozarks (Arkansas, Missouri), Midwest (Illinois, Indiana, Ohio, Wisconsin), and Southeast (see fig. 12.2 (map), p. 208 in Baskin & Baskin, 1999) has been interpreted to mean that cedar glade vegetation is the same in the three regions (cf. Curtis, 1959; Küchler, 1964). However, cedar glades of the southeastern United States are dominated by C₄ summer annual grasses, primarily *Sporobolus vaginiflorus*, and those of the Ozarks/Midwest are dominated by C₄ perennial grasses, primarily *Schizachyrium scoparium* (Baskin et al., 1994, 1995). In a recent review of the literature on cedar glades of the southeastern United States, Baskin and Baskin (1999) concluded that: (1) *Sporobolus vaginiflorus* is the most important species in this limestone/dolomite rock outcrop vegetation type; and (2) neither *Schizachyrium scoparium* nor any other perennial grass species is an important component of the vegetation. No such review of quantitative information has been published on the vegetation of calcareous glades in the Ozarks and/or Midwest.

Thus, the purpose of this paper is to review the literature on the vegetation of limestone and dolomite glades in the Ozarks and Midwest. In particular, quantitative and/or qualitative evidence is presented that, indeed, *Schizachyrium scoparium* is

¹ We thank Kayri Havens and several anonymous reviewers for their very helpful comments on various drafts of the manuscript.

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Figure 1. *Top*, Valley View Glade, Jefferson County, Missouri. *Bottom*, a glade in the Hercules Glades Wilderness Area, Taney County, Missouri. Photographs taken by Carol C. Baskin on 24 July 1996 (top) and 26 July 1993 (bottom).

the dominant plant species of these calcareous glades and that annual grasses are relatively unimportant. In addition, this review contrasts the calcareous glades of the Ozarks and Midwest with those of the southeastern United States.

THE OZARKS

Steyermark (1940; see also Steyermark, 1959) recognized five climax vegetation associations (sensu the polyclimax theory) of the Missouri Ozarks and qualitatively described stages in primary succession leading to each of them. He also recognized several subclimaxes in these seres. However, these presumed successional sequences probably represent vegetation sequences along environmental gradients that are unrelated to succession per se.

The open limestone and dolomite glades of the Missouri Ozarks are the first two stages of what Steyermark (1940) presented as a six-stage sere beginning on bare, rocky slopes and ending with a sugar maple–white oak climatic climax: (1) *Bouteloua curtipendula* (Michx.) Torr.–*Rudbeckia missouriensis* Engelm.; (2) *Rhus aromatica* Ait.–*Diospyros virginiana* L.–*Juniperus virginiana* L. (with a redcedar subclimax persisting on eroded limestone slopes and knobs); (3) *Bumelia lanuginosa* (Michx.) Pers.–*Viburnum rufidulum* Raf.; (4) *Ulmus alata* Michx.–*Rhamnus caroliniana* Walt.; (5) *Quercus muhlenbergii* Engelm.–*Fraxinus americana* L. (with *Q. muhlenbergii* forming a subclimax on southern and western exposures); and (6) *Acer saccharum* Marsh.–*Quercus alba* L. Climax vegetation in the White River region of southwestern Missouri may be *Q. muhlenbergii*–*Cotinus obovatus* Raf. Thus, the pioneer stage in this sere is a limestone (or dolomite) glade (sensu Steyermark, 1940: 392) "... with largely a component of prairie species. ..." The dominants are *Bouteloua curtipendula* and *Rudbeckia missouriensis* (*B. curtipendula*, *Psoraleidium tenuiflorum* (Pursh) Rydb., and *Silphium laciniatum* L., or *Andropogon gerardii* Vit. and *B. curtipendula* in some parts of the Ozarks). In addition to *A. gerardii* and *B. curtipendula*, other important C₄ grasses on these glades are: *Panicum virgatum* L., *Sorghastrum nutans* (L.) Nash, *Schizachyrium scoparium*, and *Sporobolus neglectus* Nash. Important forbs include *Agave virginica* (L.) Rose, *Allium stellatum* Roth., *Aster oblongifolius* Nutt., *Calamintha arkansana* (Nutt.) Shinn., *Dalea purpurea* Vent., *Echinacea pallida* (Nutt.) Nutt., *E. paradoxa* (Norton) Britt. var. *paradoxa* (an Ozark cedar glade endemic), *Hedyotis nigricans* (Lam.) Fosb., *Heliotropium tenellum* (Nutt.) Torr., *Oenothera macrocarpa* Nutt. subsp. *macrocarpa*, and *Polytaenia nut-*

tallii DC. *Berchemia scandens* (Hill) K. Koch is a common woody vine in this pioneer stage in the southwestern Ozarks.

A second seral stage begins when *Rhus aromatica*, *Diospyros virginiana*, *Juniperus virginiana*, and other woody plants invade these limestone (or dolomite) glades. *Juniperus virginiana* typically becomes the most conspicuous plant, especially on eroded slopes and "bald knobs," forming what Steyermark referred to as "cedar glades," "red cedar glades," or "red cedar balds." These terms indicate scattered redcedar trees in a matrix of herbaceous vegetation dominated by prairie grasses, in particular *A. gerardii*, *P. virgatum*, and *S. scoparium*. In the White River region of southwestern Missouri, *J. virginiana* and/or *D. virginiana* may invade limestone glades and become the dominant species. *Sassafras albidum* (Nutt.) Nees may co-occur with *D. virginiana* as a pioneer woody species.

Other investigators also have found that prairie grasses are the dominants of cedar glades in the Ozarks of Missouri. Kucera and Martin (1957) reported *Schizachyrium scoparium* as the dominant species (85% frequency, 51% of herbaceous cover) in cedar glades in the Ozarks of southwestern Missouri. Locally dominant grasses included *A. gerardii*, *B. curtipendula*, *P. virgatum*, *Sorghastrum nutans*, *Sporobolus heterolepis* (A. Gray) A. Gray, *Tridens flavus* (L.) A. Hitchc., and the C₄ summer annual *Sporobolus neglectus*. *Hedyotis nigricans* was the most important herbaceous dicot, *Rhus aromatica* the most common shrub, and *Juniperus virginiana* the most common tree. Other typical woody species included *Bumelia lanuginosa*, *Cotinus obovatus*, *Diospyros virginiana*, *Ilex decidua* Walt., and *Rhamnus caroliniana* Walt. Hicks's (1981) results of a vegetational analysis of seven stands of open cedar glades with < 30% woody plant canopy cover (stages 1 and 2 in Steyermark's scheme of xerarch succession to a sugar maple–white oak climax) in the Hercules Glades Wilderness Area in southwestern Missouri were quite similar to those of Kucera and Martin (1957). *Schizachyrium scoparium* was the dominant species, and *H. nigricans*, *Rhus aromatica*, and *J. virginiana* were the most important herbaceous dicot, shrub, and tree, respectively (Table 1). *Schizachyrium scoparium* had the highest percent importance value (%I.V.) in all seven stands sampled by Hicks.

Hall (1955) determined frequency of herbs + seedlings and of sprouts of woody plants 0.27 m or less in height and the number of *Juniperus virginiana* seedlings/saplings in an open dolomite glade in the Missouri Botanical Garden's Shaw Arboretum, near the northeastern border of the Ozark Pla-

Table 1. Average percent importance values (%I.V.) for herbs, shrubs/vines, and trees in seven stands of open cedar glades in the Ozarks of southwestern Missouri. Only plants with a %I.V. of $\geq 1.0\%$ are listed. Percent constancy and %I.V. were calculated from data in J. L. Hicks (1981).

Species	% constancy	%I.V
HERBS		
<i>Schizachyrium scoparium</i> (Michx.) Nash	100	29.21
<i>Hedyotis nigricans</i> (Lam.) Fosb.	100	10.47
<i>Sporobolus neglectus</i> Nash	100	9.47
<i>Carex</i> sp.	100	7.37
<i>Rudbeckia missouriensis</i> Engelm.	100	7.30
<i>Panicum virgatum</i> L.	100	6.40
<i>Croton capitatus</i> Michx./ <i>C. monanthogynus</i> Michx.	100	5.10
<i>Sorghastrum nutans</i> (L.) Nash	100	3.81
<i>Andropogon gerardii</i> Vit.	71	2.57
<i>Tragia betonicifolia</i> Nutt./ <i>T. ramosa</i> Torr.	100	1.73
<i>Silphium terebinthinaceum</i> Jacq.	71	1.51
<i>Sporobolus heterolepis</i> (A. Gray) A. Gray	86	1.44
<i>Palafoxia callosa</i> (Nutt.) Torr. & A. Gray	71	1.41
<i>Evolvulus nuttallianus</i> Roemer & Schultes	57	1.31
<i>Heliotropium tenellum</i> (Nutt.) Torr.	86	1.31
<i>Oenothera macrocarpa</i> Nutt. subsp. <i>macrocarpa</i>	86	1.17
<i>Dalea purpurea</i> Vent.	86	1.11
104 other species		9.18
Total		101.87
SHRUBS/VINES		
<i>Rhus aromatica</i> Ait.	100	58.77
<i>Symphoricarpos orbiculatus</i> Moench	86	9.71
<i>Berchemia scandens</i> (Hill) K. Koch	43	7.24
<i>Rosa setigera</i> Michx.	57	5.40
<i>Andrachne phyllanthoides</i> (Nutt.) J. Coulter	14	5.34
<i>Mimosa quadrivalvis</i> L.	29	4.99
<i>Vitis aestivalis</i> Michx.	57	4.84
<i>Smilax bona-nox</i> L.	57	2.10
<i>Parthenocissus quinquefolia</i> (L.) Planch.	29	1.37
<i>Toxicodendron radicans</i> (L.) Kuntze	14	0.37
Total		100.13
TREES		
<i>Juniperus virginiana</i> L.	100	41.17
<i>Cotinus obovatus</i> Raf.	100	19.17
<i>Diospyros virginiana</i> L.	86	12.15
<i>Bumelia lanuginosa</i> (Michx.) Pers.	100	6.84

Table 1. Continued.

Species	% constancy	%I.V
<i>Rhamnus caroliniana</i> Walt.	86	4.77
<i>Celtis tenuifolia</i> Nutt.	100	4.43
<i>Fraxinus americana</i> L.	71	3.67
<i>Cornus drummondii</i> C. Meyer	57	1.96
<i>Cercis canadensis</i> L.	43	1.54
<i>Quercus prinoides</i> Willd.	29	1.30
6 other species		3.09
Total		100.09

teau. Understory species with the highest frequencies were *Sporobolus neglectus* (100%), *Carex crawei* Dewey (90%), *Schizachyrium scoparium* (80%), *Hedyotis nigricans* (75%), *Euphorbia corollata* Engelm. (60%), and *Rudbeckia missouriensis* (55%). The total number of juniper seedlings in the glade was 6694, and 99.7% of these were in the 0.46-m or less height class. Average number of juniper seedlings per m² was 0.84. Hall (1955: 177) stated, "The Glade is a 'prairie' association with *Andropogon scoparius* [= *S. scoparium*] and *Rudbeckia missouriensis* contributing most to its aspect and *Andropogon scoparius* and *Sporobolus neglectus* contributing most to cover." Hall concluded that this dolomite glade was an edaphic subclimax, as did Erickson et al. (1942) for the dolomite glades of the northeastern Ozarks in general.

The flora and qualitative community ecology of limestone and dolomite glades (as well as that of sandstone, chert, and igneous glades) of the Missouri Ozarks have been studied extensively by Nelson and Ladd (1982, 1983) and Nelson (1985). Nelson and Ladd (1982: 5) stated, "Characteristic dominant vascular plants of these [dolomite] glades include *Andropogon scoparius*, *Bouteloua curtipendula*, and *Sorghastrum nutans*"; and for limestone glades, "Dominant vascular plants on these glades are *Andropogon scoparius* and *Bouteloua curtipendula*" (Nelson & Ladd, 1982: 5). Nelson (1985) listed *A. scoparius* and *B. curtipendula* as the dominant plants on limestone glades and *A. scoparius*, *B. curtipendula*, and *Sporobolus heterolepis* as dominants on dolomite glades.

Ver Hoef et al. (1993) quantitatively sampled the vegetation of 32 glades on Eminence and Gasconade dolomites in southeastern Missouri. *Schizachyrium scoparium* clearly was the most important species in these rocky forest openings. This C₄ perennial grass had a constancy of 100% in glades on each of the two geologic formations, and it was in the highest cover class (4, average % cover = 31.6) in all 32

glades, i.e., 10–100% cover class, geometric mean = 31.6. Other important species on the dolomite glades were *Andropogon gerardii*, *Calamintha arkansana*, *Carex meadii*, *Coreopsis lanceolata* L., *Echinacea pallida*, *Fimbristylis puberula* (Michx.) M. Vahl var. *puberula*, *Hedyotis nigricans*, *Liatris aspera* Michx., *Liatris cylindracea* Michx., *Panicum virgatum*, *Rudbeckia missouriensis*, *Silphium terebinthinaceum* Jacq., *Smilax bona-nox* L., *Sorghastrum nutans*, *Sporobolus clandestinus* (Biehler) A. Hitchc., and *S. vaginiflorus*. The most important woody species on these glades were *Juniperus virginiana*, *Bumelia lanuginosa*, *Diospyros virginiana*, *Pinus echinata* Miller, *Quercus prinoides* Willd., *Q. stellata* Wangenh., and *Ulmus alata*.

Keeland (1978) quantitatively sampled the vegetation of 13 calcareous glades in the Ozarks of northwestern Arkansas. He recognized four general community types, which in an apparent successional sequence are: (1) grass and cedar; (2) cedar; (3) cedar-hardwood; and (4) hardwood. Keeland (1978: 12) described the grassland-cedar type as "... a grassy slope with a few scattered woody species." Further, it "... is the typical Ozark cedar glade as described by Hall (1955) and Kucera and Martin (1957) in Missouri and Hite (1959) in Arkansas" (Keeland 1978: 9). For the representative stand of this type described by Keeland, *Juniperus virginiana* and *Quercus stellata* were the most important overstory trees, *Rhus glabra* L. the most important shrub, and *Schizachyrium scoparium* the most important herb. Overstory tree basal area on this cedar glade was low, ca. 4.8m²/ha. *Schizachyrium scoparium* also was the most important species in limestone cedar glades quantitatively sampled by Logan (1992) in the Buffalo National River area in the Ozarks of northwestern Arkansas (Table 2).

Skinner (1979) placed 0.01-m² and 0.1-m² quadrats around individual plants of the Ozark cedar glade endemic *Penstemon cobaea* Nutt. var. *purpureus* Pennell, *Centaurium texense* (Griseb.) Fern., and *Stenosiphon linifolius* (Nutt.) Heynh. to determine species associates (as well as other site characteristics) of these three rare plant species in limestone glades of the southwestern Missouri Ozarks. *Sporobolus neglectus* had the highest percent occurrence in quadrats of both sizes placed around *Penstemon* and *Centaurium*, and *Schizachyrium scoparium* had the highest percent occurrence in those of both sizes placed around *Stenosiphon*, which grows in deeper soil (15.7 ± 6.1 cm, mean ± SD) than *Penstemon* (10.9 ± 5.6 cm) or *Centaurium* (5.3 ± 2.8 cm). Percent occurrence of *S. scoparium* was considerably higher in the 0.1-m² than in the 0.01-m² quadrats: 22 vs. 5, 37 vs. < 5,

Table 2. The most important species in 20 limestone glades studied by Logan (1992) in northwest Arkansas. Only species with a presence of at least 50% and/or an average abundance of at least 1.00 are included in the list. Percentage presence and average abundance values were calculated from data in Logan (1992).

Species	Average abundance value ^a	% presence
<i>Schizachyrium scoparium</i> (Michx.) Nash	4.60	95
<i>Juniperus virginiana</i> L.	2.60	70
<i>Helianthus hirsutus</i> Raf.	2.05	70
<i>Andropogon gerardii</i> Vit.	2.00	55
<i>Quercus stellata</i> Wangenh.	1.95	60
<i>Ulmus alata</i> Michx.	1.65	70
<i>Quercus prinoides</i> Willd.	1.40	60
<i>Croton monanthogynus</i> Michx.	1.35	60
<i>Opuntia humifusa</i> (Raf.) Raf.	1.25	60
<i>Eupatorium altissimum</i> L.	1.25	45
<i>Coreopsis tinctoria</i> Nutt.	1.15	30
<i>Dichanthelium acuminatum</i> (Sw.) Gould & Clark	1.15	40
<i>Fraxinus americana</i> L.	1.15	50
<i>Ruellia humilis</i> Nutt.	1.15	60
<i>Lespedeza capitata</i> Michx.	1.10	40
<i>Sporobolus vaginiflorus</i> (Torr. ex Gray) Wood	1.10	30
<i>Dalea purpurea</i> Vent.	1.10	55
<i>Echinacea pallida</i> (Nutt.) Nutt.	1.05	40
<i>Euphorbia corollata</i> Engelm.	1.00	55
<i>Rhus aromatica</i> Ait.	1.00	55
<i>Desmanthus illinoensis</i> (Michx.) MacMillan ex Robins. & Fern.	1.00	35
<i>Bumelia lanuginosa</i> (Michx.) Pers.	0.90	50
<i>Celtis tenuifolia</i> Nutt.	0.85	50

^a Abundance scale from 1 to 5: 1 = rare (only one or two individuals present); 2 = occasional; 3 = frequent; 4 = common; and 5 = abundant (widespread with high cover, a dominant or near-dominant).

and 59 vs. 16 for *Penstemon*, *Centaurium*, and *Stenosiphon*, respectively. The increase in percent occurrence of *S. neglectus* with increase in size of quadrats was less dramatic: 46 vs. 32, 58 vs. 33, and 11 vs. 10 for *Penstemon*, *Centaurium*, and *Stenosiphon*, respectively (Skinner, 1979).

In a dolomite glade in the Ozarks of southeastern Missouri, two contiguous 7 × 7-m sample plots within a whole-glade sample unit of 100 contiguous 7 × 7-m plots dominated by *Schizachyrium scoparium* and classified as "glades" (i.e., open glades) were divided into 200 70 × 70-cm plots (Ver Hoef et al., 1993). At this small scale of sampling, the glade was divided into rocky glade, shallow soil glade, glade, and deep soil glade zones. *Sporobolus*

vaginiflorus was the dominant species in the rocky glade and shallow soil glade zones, and *S. scoparium* in the glade and deep soil glade zones (Ver Hoef et al., 1993). However, in two other dolomite glades in southeastern Missouri sampled by Ver Hoef et al. (1993), as described above, *S. vaginiflorus* was not an important species.

Results of studies by Skinner (1979) and Ver Hoef et al. (1993) support a statement made by Kucera and Martin (1957: 290) in their study of glades in the Ozarks of southwestern Missouri: "*Andropogon scoparius* [= *Schizachyrium scoparium*] was the principal dominant; *Sporobolus neglectus* was generally frequent and locally abundant." Hall (1955), Hicks (1981), and Logan (1992) also found that either *Sporobolus neglectus* or *S. vaginiflorus* was a relatively important species in the Ozark glades they studied. Nelson (1985) listed *S. neglectus* as a characteristic plant of dolomite glades, but not of limestone glades, in the Ozarks of Missouri. Thus, both quantitative and qualitative studies show that annual *Sporobolus* species can be locally dominant within the larger prairie-like community on limestone and dolomite glades in the Ozarks. As such, cedar glades of the type described for the southeastern United States (Baskin & Baskin, 1999) occur in microhabitats within xeric limestone prairies of the Ozarks.

Schizachyrium scoparium also is the dominant plant in Ozark glades in terms of dry mass production. In the Ozarks of southwestern Missouri, total annual herbage production on glades ungrazed for 4 and 21 years was 312.2 and 241.5 g/m², respectively, according to a study by Buttery (1960). Production by *S. scoparium* on these two exclosures (the term used by Buttery to mean areas fenced off to prevent cattle grazing) was 175.2 and 112.3 g/m², respectively, and by *Sporobolus neglectus* 24.7 and 7.9 g/m², respectively. In the 4-year exclosure, production by *Andropogon gerardii* and *Sorghastrum nutans* was 52.2 and 34.8 g/m², respectively, and in the 21-year exclosure 29.2 and 74.7 g/m², respectively. Thus the C₄ perennial grasses *S. scoparium*, *A. gerardii*, and *S. nutans* produced 84% and 89% of the total herbage on the 4- and 21-year exclosures, respectively (Buttery, 1960). Regarding herbage production on grazed glades, Buttery (1960: 235) stated, "In 1956, as now, the glades outside the exclosures were producing about 400 pounds of oven dry herbage per acre [44.9g/m²], mostly the less desirable baldgrass [*S. neglectus*] and black-eyed Susan (*Rudbeckia hirta* L.) with a scattering of the more desirable little bluestem (*Andropogon scoparius* Michx.) and Indiangrass [*S.*

nutans]." Thus, annual *Sporobolus* can be the dominant grass on overgrazed Ozark glades.

THE MIDWEST

In the Midwest, cedar or limestone glades have been reported in Wisconsin, Illinois, and Indiana. *Schizachyrium scoparium* was the most prominent ground-layer species in what Curtis (1959) called cedar glades in Wisconsin, with a presence of 100% and an average frequency of 38%. Other species in the ground layer with relatively high values for presence and average frequency were the C₃ herbaceous perennial forbs *Aquilegia canadensis* L., *Anemone cylindrica* A. Gray, *Dalea purpurea*, *Tradescantia ohioensis* Raf., *Euphorbia corollata*, *Arenaria stricta* Michx., *Solidago nemoralis* Dryander, *Antennaria neglecta* E. Greene, *Viola pedata* L., and *Scutellaria leonardii* Epling; the C₄ perennial grasses *Andropogon gerardii*, *Bouteloua hirsuta* Lagasca, and *Bouteloua curtipendula*; and the C₃ perennial grass *Koeleria pyramidata* (Lam.) P. Beauv. (Curtis, 1959: table XVI-10, appendix, p. 573). The most important tree species was *Juniperus virginiana* (Curtis, 1959: table XVI-11, appendix, p. 574).

Schizachyrium scoparium had a frequency of 80–100% in 30 of 32 limestone glades sampled by Kurz (1981) in Illinois. Other important grasses were the C₄ perennials *Bouteloua curtipendula*, *Sorghastrum nutans*, and *Sporobolus aspera* (Michx.) Kunth. The important forbs were the CAM leaf succulent *Agave virginica*; the C₃ perennials *Aster oblongifolius*, *Brickellia eupatorioides* (L.) Shinn., *Echinacea pallida*, *Euphorbia corollata*, *Hedyotis nigricans*, and *Physostegia virginiana* (L.) Benth.; and the C₃ summer annual *Croton monanthogynus* Michx. *Schizachyrium scoparium* also was the most important species in the limestone glades of southern Illinois studied by Heikens and Robertson (1995).

Limestone glades have been reported from five counties in southern Indiana (Aldrich et al., 1982; Bacone et al., 1983; Homoya, 1987; Maxwell, 1987), and they obviously are dominated by perennial prairie grasses. For example, referring to a limestone glade in Perry County, Bacone et al. (1983: 368) stated, "Indian grass (*Sorghastrum nutans*), big bluestem (*Andropogon gerardii*) and little bluestem (*A. scoparius*) are common grasses." Referring to two cedar glades in Clark County, Maxwell (1987: 413) stated, "Little bluestem dominates both glades as a xeric, bunch-grass surrounded by patches of rocky pavement."

The Ozarks and Midwest limestone and dolomite glades described above are similar vegetationally to

Table 3. Average percent frequency of native plant taxa in 147 1 × 1-m quadrats in five stands of xeric prairie vegetation on the Peebles dolomite in Adams County, Ohio. Only plants with a frequency of ≥20% are listed (calculated from data in Braun, 1928).

Species	% frequency
<i>Schizachyrium scoparium</i> (Michx.) Nash	79.4
<i>Euphorbia corollata</i> Engelm.	53.6
<i>Blephilia ciliata</i> (L.) Benth.	50.8
<i>Lithospermum canescens</i> (Michx.) Lehm.	45.2
<i>Agave virginica</i> (L.) Rose	43.2
<i>Ruellia humilis</i> (Nees) Lindau	41.8
<i>Silphium trifoliatum</i> L.	38.2
<i>Bouteloua curtipendula</i> (Michx.) Torr.	32.4
<i>Thaspium</i> sp.	32.0
<i>Pycnanthemum flexuosum</i> (Walt.) Britton, Sterns & Poggenb.	29.8
<i>Senecio plattensis</i> Nutt.	29.4
<i>Sorghastrum nutans</i> (L.) Nash	29.0
<i>Comandra umbellata</i> (L.) Nutt.	27.6
<i>Helianthus hirsutus</i> Raf.	27.6
<i>Andropogon gerardii</i> Vit.	26.2
<i>Zizia aptera</i> (A. Gray) Fern.	25.4
<i>Fragaria vesca</i> L.	25.2
<i>Prunella vulgaris</i> L.	23.4
<i>Delphinium exaltatum</i> Ait.	23.2
<i>Lobelia spicata</i> Lam.	22.8
<i>Scutellaria parvula</i> Michx.	21.4
<i>Solidago nemoralis</i> Ait.	20.0

what Braun (1928) called xeric prairies on Silurian Dolomite in Adams County in southern Ohio. Here, prairie grasses, primarily *Schizachyrium scoparium*, also are the dominant plants (Table 3). Interestingly, Braun pointed out that although there is some overlap in species composition between the xeric prairies of Adams County and the cedar glades of the Nashville Basin, the vegetation is different.

Neither annual species of *Sporobolus* nor of other grasses seem to be an important component of cedar or limestone glades that have been sampled quantitatively in Wisconsin (Curtis, 1959) or Illinois (Kurz, 1981; Heikens & Robertson, 1995). However, in one of the xeric prairies, Agave Ridge, on Silurian dolomite in Adams County, Ohio, sampled by Braun (1928), *S. vaginiflorus* had a frequency of 68% in 25 1-m² quadrats. The dominants of this prairie were *Schizachyrium scoparium* (100% frequency) and *Bouteloua curtipendula* (84% frequency). Braun referred to Agave Ridge and one of the four prairies she sampled on Peebles Dolomite as being more xerophytic than the other three. However, the average frequency of *S. vaginiflorus* on the five Peebles dolomite prairies was only 14.8%. Neither is *S. vaginiflorus* an important

component of the vegetation of limestone glades in Indiana (Aldrich et al., 1982; Bacone et al., 1983; Homoya, 1987; Maxwell, 1987).

WOODY PLANT INVASION INTO OZARK AND
MIDWEST GLADES

Martin (1955: 106) stated that "... even the thin-soiled areas [in the Ozarks of southwestern Missouri] are being invaded by eastern redcedar (*Juniperus virginiana*), winged elm (*Ulmus alata*), and associated drought-tolerant trees." Using 1938 and 1975 USDA aerial photographs showing limestone and dolomite glades in southwestern Missouri, Kimmel and Probasco (1980) found a dramatic decrease in glade area with 0–15% woody cover and a corresponding increase in glade area with 50–100% woody cover. Lowell and Astroth (1989) used USDA aerial photographs to study natural succession of glades to forest in the Hercules Glades Wilderness Area (southwestern Missouri) from 1938 to 1986. They found that "Even those areas most favorable for glades [Gasconade soil, 305–365 m (a.m.s.l.), south or southwest slopes] continue to convert to forest" (Lowell & Astroth, 1989: 78). The area most favorable for glades and occupied by glades decreased from about 285 ha to about 200 ha (30%) via conversions of glade land to forest (see fig. 3 in Lowell & Astroth, 1989). Using 1955, 1966, and 1984 aerial photographs, Ver Hoef et al. (1993) also showed that the sizes of dolomite glades in the Ozarks of southeastern Missouri had decreased due to woody plant invasion.

Kimmel and Probasco (1980) concluded that the most important reason for the increase in woody plant cover on open glades between 1938 and 1975 was that the U.S. Forest Service had not used fire to manage glade (cattle) range. Lowell and Astroth (1989: 78) thought that their study "... appears to support the theory held by some ecologists (USFS, pers. comm.) that the glades are not a naturally occurring ecotype[?] which can maintain themselves independent of fire and/or human intervention." Likewise, Ver Hoef et al. (1993) attributed woody plant invasion into calcareous glades in southeastern Missouri to fire suppression. Fire frequency was high in the Missouri Ozarks in presettlement times (Guyette & McGinnis, 1982), and fire probably played an important role in the origin and maintenance of limestone and dolomite glades in that area.

According to Curtis (1959), cedar glades in Wisconsin: (1) may have originated by invasion of redcedar into a dry prairie on sites protected from fire; and (2) would in time succeed to oak forest.

Heikens (1991) speculated that, in the absence of fire, the perennial grass-dominated limestone glades in southern Illinois would succeed to barrens ("savannas") and then to forest.

By studying aerial photographs of limestone glade areas in southern Indiana, Aldrich et al. (1982) and Bacone et al. (1983) determined that these openings in the forest are decreasing in size. Aldrich et al. (1982: 484) stated, "Aerial photographs document the continuing shrinkage of these glades [in Harrison County], as they were nearly double their present size in the 1940s." Bacone et al. (1983: 372) stated, "The aerial photographs show a remarkable decrease in size [of the forest openings in Perry County] in the last forty years due to encroachment of woody species."

Braun (1928: 425) thought the xeric prairies in Adams County, Ohio, "... antedate settlement by white man and are undoubtedly primary." However, using USDA aerial photographs taken in 1938, 1950, 1965, and 1971, Annala et al. (1983) and Annala and Kapustka (1983) found that prairie has succeeded (is succeeding) to forest. For example, prairie openings in the Lynx Prairie Preserve, where the soils are "shallow and poorly developed" (Annala et al., 1983: 22), covered 47% of the Preserve in 1938 but only 16% in 1971 (Annala et al., 1983; also see Foré & Guttman, 1996). Based on lack of difference in opal (phytolith) mass between soils presently under prairies and those presently under cedar-hardwood forests on dolomite in Adams County, Boettcher and Kalisz (1991: 127) concluded that "... the long-term vegetative history has been generally uniform over all areas on dolomite regardless of present occupancy by prairie or forest." Further, "... the distinction between primary and secondary prairies has little meaning since prairies only occur on areas of dolomite, and prairies and forest have alternated over time on these areas" (Boettcher & Kalisz, 1991: 127).

CONCLUDING REMARKS

The vegetation of limestone and dolomite glades in the Ozarks and Midwest is dominated by C_4 perennial prairie grasses (primarily *Schizachyrium scoparium*), and burning or some other method for removal of woody plant invaders is required to prevent succession to forest in these rocky, calcareous openings. Thus, they differ from cedar glades in the southeastern United States, in which the dominants are C_4 summer annual grasses (primarily *Sporobolus vaginiflorus*), and succession to forest does not occur in the absence of burning or other forms of management (Baskin & Baskin, 1999). The struc-

ture of the vegetation of the limestone and dolomite glades in the Ozarks and Midwest is much more similar to the xeric prairies on Silurian dolomite described by Braun (1928) in Adams County, Ohio, and to the xeric prairies on Mississippian limestone described by Baskin et al. (1994) on and adjacent to the Kentucky Karst Plain, than it is to what traditionally has been called cedar glades in the southeastern United States. Küchler's (1964) vegetation map of the United States shows the same vegetation type for cedar glades in the Ozarks and in middle Tennessee-northern Alabama. However, ample evidence is available in the literature to show that the glade vegetation of these two regions is quite different. Thus, we suggest that the rocky, calcareous, anthropogenic, prairie-grass-dominated openings in the Ozarks and Midwest be called xeric limestone prairies, in contrast to cedar glades, which are an edaphic climax dominated by C_4 summer annual grasses.

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